

NOTES ON THE HOST, EGG, AND PUPARIUM OF
STYLOGASTER BIANNULATA (SAY) (DIPTERA: CONOPIDAE)

NORMAN E. WOODLEY AND DARLENE D. JUDD

(NEW) Systematic Entomology Laboratory, PSI, Agricultural Research Service, U.S. Department of Agriculture, % National Museum of Natural History, MRC-168, Washington, DC 20560, U.S.A. (e-mail: nwoodley@sel.barc.usda.gov); (DDJ) Department of Entomology, Smithsonian Institution, MRC-169, Washington, DC 20560, U.S.A.

Abstract.—The egg and puparium of *Stylogaster biannulata* (Say) (Diptera: Conopidae) are described and illustrated in detail based on examination by scanning electron microscopy. This species was reared from *Gryllus rubens* Scudder in Florida, a new host record. Previous literature is reviewed in light of this new data.

Key Words: *Stylogaster biannulata*, Conopidae, hosts, egg, puparium, *Gryllus rubens*

The genus *Stylogaster* Macquart has about 85 species distributed primarily in tropical regions in both hemispheres (Smith 1979: fig. 1). The greatest diversity is in the New World where 63 species occur (Camras and Parrillo 1985), two of which are found in the Nearctic Region. This paper reports new data on hosts and immature stages for *Stylogaster biannulata* (Say) which occurs from Rhode Island to Nebraska, south to Texas, Florida, and Veracruz, Hidalgo, and San Luis Potosi in Mexico (Camras 1965, Camras and Parrillo 1985). The other Nearctic species, *S. neglecta* Williston, is known from Massachusetts to Nebraska, south to Arizona, Georgia, and Sinaloa and Chiapas in Mexico; its biology remains completely unknown.

HOSTS OF *STYLOGASTER*

The enigmatic biology of *Stylogaster* has been the subject of much speculation ever since Bates (1863: 365) published one of the first natural history observations of *Stylogaster* females hovering over advancing swarm raids of army ants of the genus *Ecton* Latreille. Early authors [see Aldrich

(1930) for a good summary] were of the opinion that *Stylogaster* must have been using army ants as hosts. Lopes (1937) found eggs of *Stylogaster* on an unspecified orthopteran and a cockroach. Later observations, particularly detailed ones by Rettenmeyer (1961), showed that the conopids were ovipositing on insects displaced by the advancing ants, as well as other insects, especially tachinid flies of the genera *Calodexia* Wulp and *Androeuryps* Beneway looking for hosts displaced by the ants. However, Rettenmeyer was of the opinion that cockroaches and possibly other orthopteroid insects were the most likely hosts of *Stylogaster*, and eggs were inserted accidentally into tachinids utilizing the same hosts. He did, however, note (1961: 1015) that one of 17 *Stylogaster* eggs found on tachinids had initiated development, so he did not completely discount tachinids as hosts. Stuckenberg (1963), Smith (1967, 1969), and Smith and van Someren (1985) discussed the occurrence of *Stylogaster* eggs on various calyprate Diptera, primarily Muscidae, in the Afrotropical Region. Some of these flies were associated with

driver ants while others were associated with animal dung (and in the latter case *Stylogaster* eggs were found on flies outside of the geographic distribution of driver ants). Stuckenberg (1963) was of the opinion that because *Stylogaster* eggs were more common on dung-breeding muscids he studied than was observed by Rettenmeyer (1961) in Panama, it was more likely that flies were the true *Stylogaster* hosts in Africa. Smith (1979) noted that *Stylogaster liepae* Smith was collected while hovering over a bird nest, and speculated that perhaps they were looking for flies attracted to dung or carrion in or near the nest.

All of the above evidence concerning *Stylogaster* hosts is circumstantial. It was not until Smith and van Someren (1985) reported dissecting larvae of *Stylogaster varifrons* Malloch from cockroach nymphs and a larva of *S. westwoodi* Smith from a gryllid cricket that unequivocal host associations were known. Adults of both species were seen ovipositing on their hosts being displaced by army ants in a garden in Kenya.

One of us (NEW) was sent a collection of Diptera reared from *Gryllus* spp. by Thomas J. Walker and his associates near Gainesville, Alachua County, Florida. While most of the specimens were Tachinidae of the genera *Ormia* Robineau-Desvoidy and *Anisia* Wulp, it was surprising to find some specimens of *Stylogaster biannulata* in the lot. Most of the *Stylogaster* specimens had been reared from *Gryllus rubens* Scudder with a couple being reared from unidentified *Gryllus*. Susan Wineriter (personal communication) provided some details about how these collections were made. The crickets were collected mostly in sound traps (Walker 1986) with some taken in pitfall traps. Crickets were held alive in the lab individually to check for parasites for up to 9 d, the main aim being to study the parasitism level in the crickets by *Ormia ochracea* (Bigot). It was estimated that about 1000 crickets were censused, and from these only 25–30 puparia of *Styl-*

ogaster biannulata were obtained. Puparia were obtained from crickets collected in May, August, September, October, November, and December. Although not observed, the larvae probably emerged from their cricket hosts because puparia were found outside the host. In a few cases more than one *S. biannulata* puparium came from a single cricket, and in at least one case *S. biannulata* and the tachinid *Anisia gilvipes* (Coquillett) successfully parasitized a single cricket. In the three cases where data were recorded, the *S. biannulata* adults emerged 19–25 days after their puparia were formed.

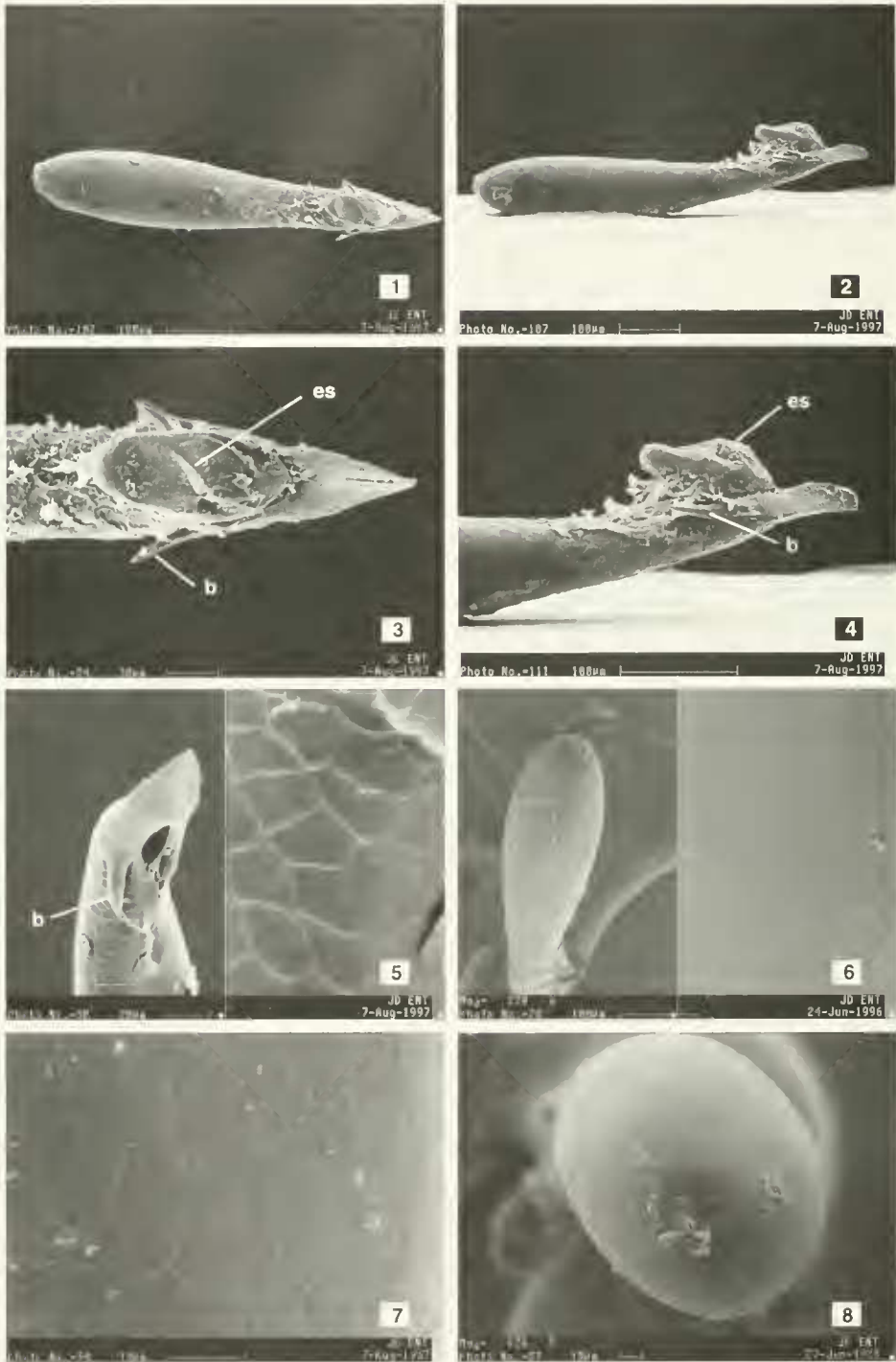
Nothing is known about how *Stylogaster biannulata* locates its host. It certainly is not dependent on above-ground army ants as they do not occur in the United States.

THE EGG OF *STYLOGASTER BIANNULATA*

The eggs of *Stylogaster* were first described by Lopes (1937). Subsequently it was discovered that the eggs have species-specific characters which have been illustrated for many species (Lopes 1938, Lopes and Monteiro 1959, Monteiro 1960, Smith 1967, 1979). The end opposite the micropyle is pointed and has subapical barbs, and this end is embedded in the insect victim at the time of oviposition. The actual mechanism of oviposition is unknown (Kotrba 1997, reviews the data on this subject).

We obtained about a dozen eggs from a female of *Stylogaster biannulata* that was collected at Lick Creek Park, Brazos County, Texas. A figure (Smith and Peterson 1987: fig. 54.25) of the egg of this species has been published but no further descriptive details were given. Because the egg has not been described in detail, we present information on its morphology, based on scanning electron microscope examination. SEMs have been published only for *S. macalpini* Smith (Smith 1979: figs. 24–25) and *S. westwoodi* (Hinton 1981: plate 119).

Description.—Clavate in shape (Fig. 1), nonmicropylar end narrow, slightly arcuate ventrally (Fig. 2), sharply pointed in ventral view (Fig. 3), blade-like in lateral view



Figs. 1-8. Egg of *Stylogaster biannulata* 1, Whole egg, ventral view. 2, Whole egg, lateral view. 3, Non-micropylar end, ventral view. 4, Non-micropylar end, lateral view. 5, Non-micropylar end, posterolateral view, with inset showing surface sculpture of adjacent area. 6, Whole egg, anterolateral view of micropylar end, with inset showing surface sculpture of egg body. 7, Surface sculpture of egg body at higher magnification. 8, Micropylar end, showing concentric surface sculpture. Abbreviations: *b*, barb; *es*, eversible sac.

(Fig. 4); with a single pair of small, lateral, subapical barbs (Figs. 3–5, *b*); small eversible sac present between bases of barbs (Figs. 3–4, *es*), when not inflated this region appearing as a cavity (Fig. 5); entire surface, except pointed end, with reticulate surface sculpturing forming irregular cells, the sculpturing strongest and appearing scale-like near barbs (Fig. 5), the cells becoming more elongate and less strongly indicated on main body (Figs. 6, 7), then small and roughly concentric around micropylar end (Fig. 8). Length 0.65 mm ($n = 1$).

Remarks.—Unfortunately the eggs we examined were embedded in glue on a point with the specimen from which they came, and we were unable to clean them completely. In hydrated specimens, the eversible sac appears regularly rounded, as in Smith and Peterson (1987: fig. 54.25), not irregular as in the SEMs. Lopes (1937) concluded that the larva enters the host through this structure. Rettenmeyer (1961) postulated that this sac was inflated when the egg was inserted into a host and helped hold the egg in place and possibly also absorbed nutrients from the host. Based on osmotic manipulations, Stuckenberg (1963) was of the opinion that the eversible sac functioned at least in part in erecting the lateral barbs. Hinton (1981) was skeptical of this theory as he thought the barbs were more or less immovable. We found some evidence to support Stuckenberg's idea. In Fig. 5, an egg in which the sac is not everted, the barbs are more closely appressed to the surface of the egg, while in Fig. 3, where the sac is everted, the barbs are more erect.

How the larva hatches from the egg is still uncertain. Rettenmeyer (1961: fig. 1) illustrated an egg found on a tachinid with a larva just emerging from the micropylar end, and therefore discounted Lopes' (1937) theory that the larva emerged through the eversible sac. Smith and van Someren (1985) also reported observing eggs that had embryos visible inside that were facing the micropyle. However, the

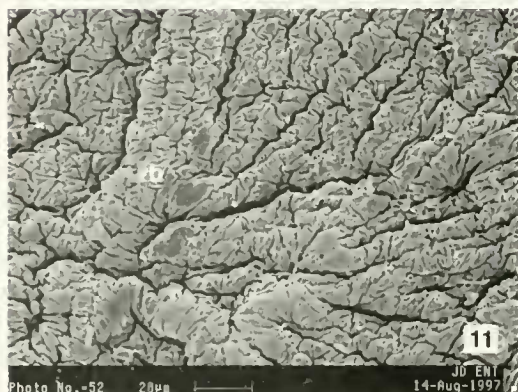
empty eggs of *S. varifrons* present on cockroach nymphs from which they dissected larvae were intact, indicating that the larvae had entered the host from near or through the sac.

THE PUPARIUM OF *STYLOGASTER BIANNULATA*

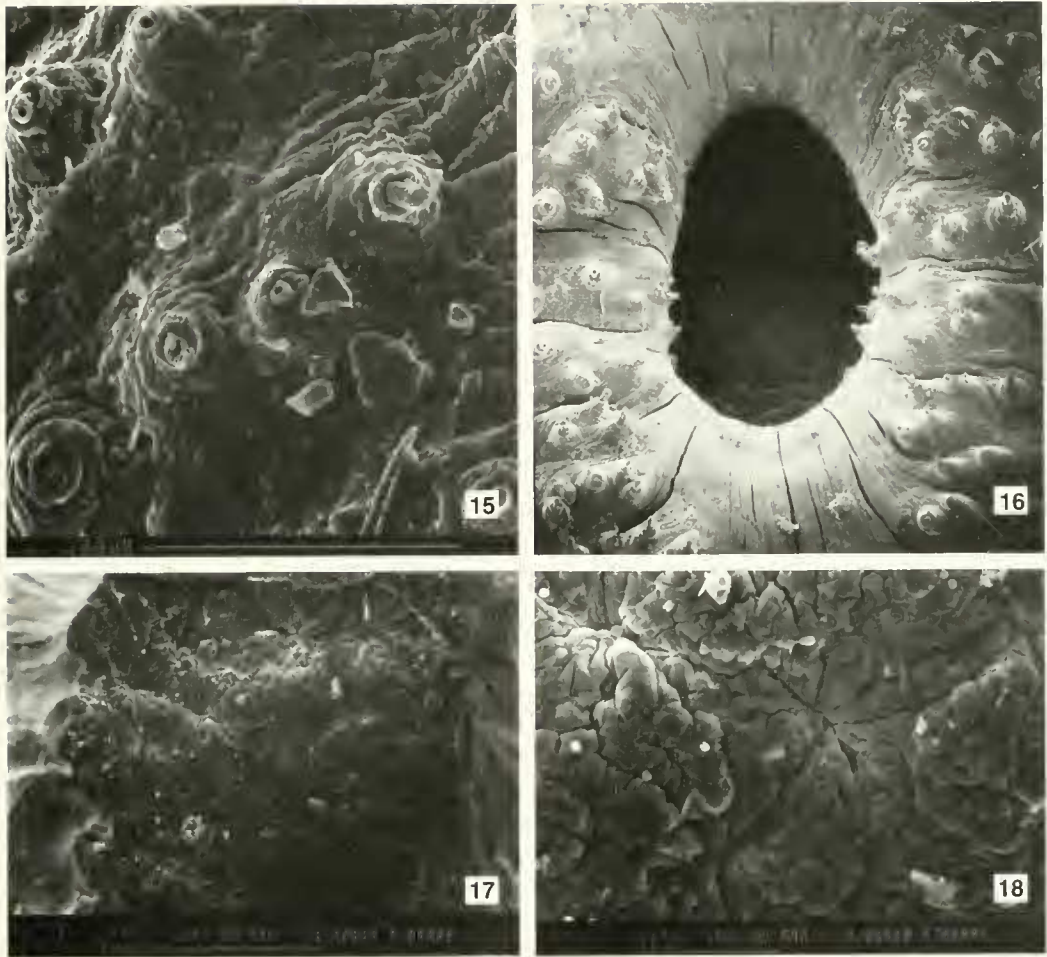
We examined 29 or 30 puparia obtained from the rearings of *S. biannulata* from *Gryllus* already discussed in the section on hosts. All specimens are now housed at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. As this life stage is unknown for any *Stylogaster*, we are describing it here.

Description.—Reddish brown to dark brown; ovoid (Fig. 9), surface finely wrinkled with crisscrossing network of slightly raised bands (Figs. 10, 11, *rb*), at higher magnification the surface appears more deeply wrinkled (Fig. 11); posterior end with lateral raised areas that are bilobed (nearly c-shaped; Figs. 12, 13), with numerous raised, cone-shaped tubercles that end in a pore (Figs. 14, 15; peg-like exudate present in many pores is apparently a result of drying); posterior end near apex with deep cavity with ovoid opening (Fig. 16); inner surface of cavity finely wrinkled (Figs. 17, 18), with larger wrinkles more or less radiating from slightly depressed points. Length 4.3–5.9 mm.

Remarks.—The structure of the puparium closely reflects the larval description provided by Smith and van Someren (1985). The bilobed, laterally raised areas on the posterior end presumably correspond to the tracheal system, and the sunken cavity on the posterior end was also noted in the larval description. We were not able to describe the larval cephalopharyngeal skeleton that is present inside the anterior end of the puparium. It is extremely small, and we were not successful in several attempts in removing it from the tissue in which it was embedded. What we could see corresponds with the larval mouthparts described by Smith and van Someren (1985: figs. 10, 11).



Figs. 9-14. Puparium of *Srylogaster biannulata*. 9, Whole puparium, lateral view. 10, Surface sculpture of main body of puparium. 11, Higher magnification view of surface sculpture of main body of puparium. 12, Posterior end of puparium, lateral view. 13, Posterior end of puparium, posterior view. 14, Conical tubercles of tracheal tissue on posterior end of puparium. Abbreviation: *rb*, raised band.



Figs. 15–18. *Stylogaster biannulata*. 15, Conical tubercles of tracheal tissue on posterior end of puparium. 16, Posterior cavity of puparium. 17, Inner surface of internal cavity of puparium. 18, Inner surface of internal cavity of puparium, higher magnification.

We consider it doubtful that the second instar larvae that Rettenmeyer (1961: 1016) speculated might be *Stylogaster* are this genus. The large mouthparts and simple posterior spiracles Rettenmeyer described are not at all like those of the larvae described by Smith and van Someren (1985) and the puparia we examined.

ACKNOWLEDGMENTS

We thank Thomas J. Walker and Susan A. Wineriter (University of Florida, Gainesville) for providing the *Stylogaster* adults

and puparia as well as information on how they were collected and reared. Robert A. Wharton (Texas A & M University, College Station) provided the specimen with eggs for our study. Walter R. Brown and Susann G. Braden (Electron Microscopy Laboratory Smithsonian Institution) assisted materially with SEM work. Steven W. Lingafelter (Systematic Entomology Laboratory) helped with scanning some of the SEM images into a more usable format. Wayne N. Mathis (Smithsonian Institution), Andrew V. Z. Brower (Smithsonian Institution),

Douglass R. Miller, and Allen L. Norrbom (Systematic Entomology Laboratory) reviewed the manuscript.

LITERATURE CITED

- Aldrich, J. M. 1930. American two-winged flies of the genus *Stylogaster* Macquart. Proceedings of the United States National Museum 78: 1-27.
- Bates, H. W. 1863. The naturalist on the Amazons: A record of adventures, habits of animals, sketches of Brazilian and Indian life, and aspects of nature under the Equator during eleven years of travel. G. Routledge & Sons, London. x + 518 pp.
- Camras, S. 1965. Family Stratiomyidae, pp. 625-632. In Stone, A. et al. eds., A catalog of the Diptera of America north of Mexico. U.S.D.A. Agriculture Handbook 276. United States Department of Agriculture, Washington, D.C. iv + 1696 pp.
- Camras, S. and P. P. Parrillo. 1985. Review of New World *Stylogaster* (Diptera: Conopidae). Annals of the Entomological Society of America 78:111-126.
- Hinton, H. E. 1981. Biology of insect eggs in three volumes. Volume 1 Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt. xxiv + 473 pp.
- Kotrba, M. 1997. Shoot or stab? Morphological evidence on the unresolved oviposition technique in *Stylogaster* Macquart (Diptera: Conopidae), including discussion of behavioral observations. Proceedings of the Entomological Society of Washington 99: 614-622.
- Lopes, H. de S. 1937. Contribuição ao conhecimento do genero "*Stylogaster*" Macquart, 1835, (Dipt. Conopidae). Archivos do Instituto de Biologia Vegetal 3: 257-293.
- . 1938. Sobre uma nova especie do genero *Stylogaster* Macquart, do Brasil (Dipt.: Conopidae). Memórias do Instituto Oswaldo Cruz 33: 403-405.
- Lopes, H. de S. and L. Monteiro. 1959. Sobre algumas espécies brasileiras de *Stylogaster* Macq., com a descrição de quatro espécies novas (Dipt., Conopidae). Studia Entomologica 2: 1-24.
- Monteiro, L. 1960. Insecta Amapaensia. Diptera: Conopidae: espécies do gênero *Stylogaster* Macquart, 1835. Memórias do Instituto Oswaldo Cruz 58: 103-114.
- Rettenmeyer, C. W. 1961. Observations on the biology and taxonomy of flies found over swarm raids of army ants (Diptera: Tachinidae, Conopidae). University of Kansas Science Bulletin 42: 993-1066.
- Smith, K. G. V. 1967. The biology and taxonomy of the genus *Stylogaster* Macquart, 1835 (Diptera: Conopidae, Stylogasterinae) in the Ethiopian and Malagasy regions. Transactions of the Royal Entomological Society of London 119: 47-69.
- . 1969. Further data on the oviposition by the genus *Stylogaster* Macquart (Diptera: Conopidae, Stylogasterinae) upon adult calyptrate Diptera associated with ants and animal dung. Proceedings of the Royal Entomological Society of London (A) 44: 35-37.
- . 1979. The genus *Stylogaster* (Diptera: Conopidae, Stylogasterinae) in the Australian Region. Australian Journal of Zoology 27: 303-310.
- Smith, K. G. V. and B. V. Peterson. 1987. Conopidae, Chapter 54, pp. 749-756. In McAlpine, J. F., ed. Manual of Nearctic Diptera. Volume 2. Agriculture Canada, Ottawa. i-vi: 675-1332.
- Smith, K. G. V. and G. R. Cunningham-van Someren. 1985. The larva of *Stylogaster varifrons* Malloch (Dipt., Stylogasteridae). Entomologist's Monthly Magazine 121: 81-85.
- Stuckenberg, B. R. 1963. A study on the biology of the genus *Stylogaster*, with the description of a new species from Madagascar (Diptera: Conopidae). Revue de Zoologie et de Botanique Africaines 68: 251-275.
- Walker, T. J. 1986. Monitoring the flights of field crickets (*Gryllus* spp.) and a tachinid fly (*Euphasiopteryx ochracea*) in north Florida. The Florida Entomologist 69: 678-685.